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Pollen eaters and pollen morphology: co-evolution through the Permian and Mesozoic

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ABSTRACT

In each of the sequential periods of seed-plant evolution, there were “charismatic” pollen grains that fascinated generations of palynologists. In the Permian, such peculiar pollen morphologies included taeniate pollen (with the wall split into bands, or taeniae) of *Protohaploxypinus–Lunatisporites* and *Vittatina* groups. One or more types of taeniate pollen prevailed in the pollen load of several species of Permian insects. The advent of the Mesozoic era was marked by a spread of smooth asaccate pollen of “*Ginkgocycadophytus*” type, virtually indistinguishable in the dominant orders of Mesozoic gymnosperms. Such pollen was never found in the guts. Charismatic through the Mesozoic was the rimulate pollen of *Classopollis* type. It constituted a monospecific load in the guts of large Jurassic katydids (*Aboilus*, Haglidae). The *Eucommiidites* group, related to gnetophytes, is peculiar in having lateral grooves parallel to the main sulcus. Recently this pollen type has been found in the gut compression of a xyelid, genus *Ceroxyela*. The reason why Palaeozoic and Mesozoic insects showed preferences for pollen with distinctive morphologies might be that, on the basis of the surface ornamentation of these different varieties, insects were able to distinguish edible pollen types. The distinctive pollen morphologies might have evolved primarily for this purpose.

KEY WORDS: Palynology, taeniate pollen, *Classopollis*, *Eucommiidites*, Grylloblattida, Hymenoptera, Hypoperlida, Orthoptera, Palaeomanteida, Psocida, co-evolution, Permian, Mesozoic.

INTRODUCTION

Pollen preserved in gut compressions of fossil insects gives direct evidence of feeding habits that played a significant role in morphological evolution of insects since the Permian (Krassilov & Rasnitsyn 1999 and elsewhere). In particular, a recent find of pollen grains in the intestines of *Sellardsiopsis conspicua* G. Zalessky (Palaeomanteida) confirms a hypothesis of pollinivory in the ancestral group of Holometabola (Rasnitsyn 1980). Yet the question remains whether or not the impact of pollen eaters on their forage plants was reciprocated. In order to test a hypothesis of co-evolution, we take a closer look at the morphology of pollen grains that met the dietary requirements of Palaeozoic and Mesozoic insects.

Both in the Permian and Mesozoic, there are rather featureless pollen grains, a nuisance for palynotaxonomists. On the other hand, there are fewer, but prominent pollen grains, readily recognizable owing to their distinctive surface features, such as taeniae, rimulae, pseudopores, pseudosulci. *Protohaploxypinus*, *Vittatina*, *Classopollis*, *Eucommiidites*, are some of the pollen varieties which are attractive as the objects of detailed morphological classification, because, with proper microscopic techniques, they display variations of their surface microstructures that seem taxonomically significant. For this same reason, they provide good stratigraphic markers, which makes them charismatic in the eyes of palynostratigraphers. Our data on pollen load of fossil insects indicate that not only palynologists, but also pollinivorous insects were attracted by pollen grains with ornamental surface patterns.

MATERIAL AND METHODS

The material was collected from rich localities of fossil plants and insects in the Lower Permian (Kungurian) of Tschekarda, the Central Cis-Urals; the Upper Jurassic of the Karatau Range, southern Kazakhstan; and the Lower Cretaceous of Baissa, Transbaikalia (Table 1; descriptions of the localities can be found in Ponomareva *et al*. 1998; Doludenko & Orlovskaya 1976; Krassilov & Bugdaeva 1999). The insect collections have been surveyed for specimens with gut contents preserved as compressions of organic matter visually distinct against the impression of the insect body due to their different microstructure and coloration. Pollen grains discernible at low magnification were picked up with thin needles under a stereomicroscope. Alternatively, they were extracted by maceration of embedding rocks. Microsamples

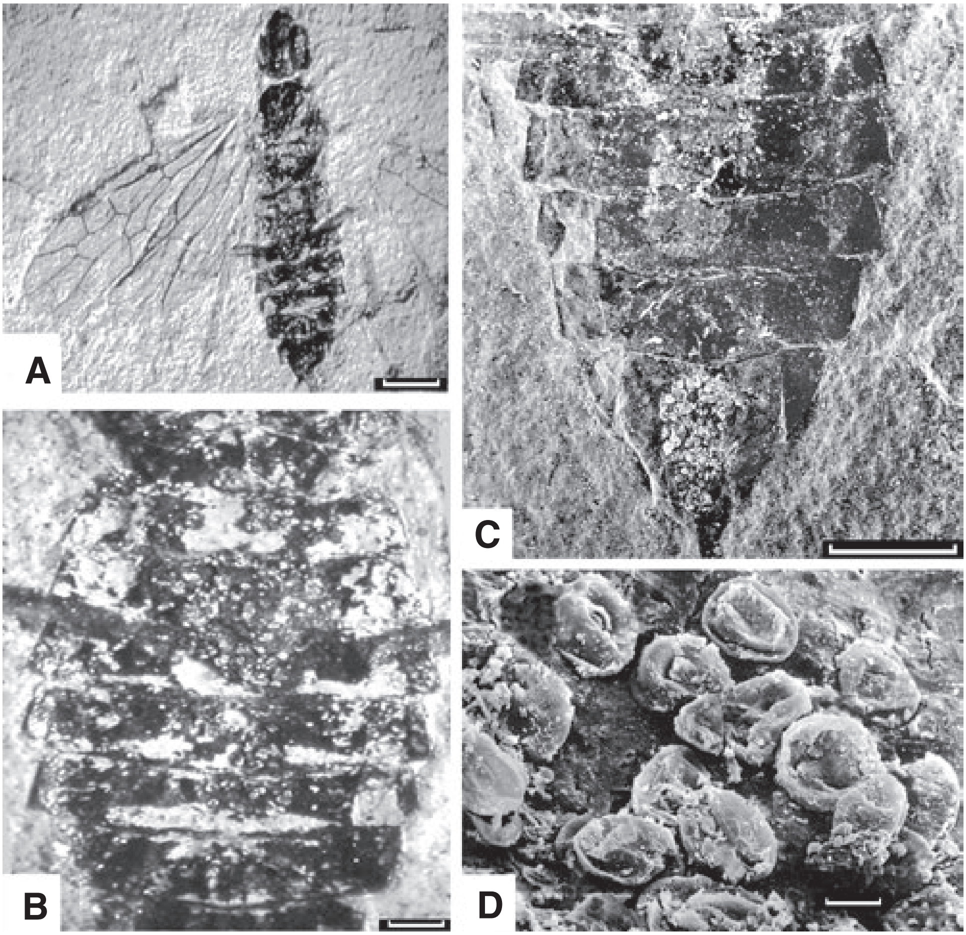

Fig. 1. *Eucommiidites* group pollen (*Cryptosaccites pabularis* Krassilov et Tekleva) in the gut compression of *Ceroxyela dolichocera* Rasnitsyn (Xyelidae, Hymenoptera) from the Lower Cretaceous of Baissa, Transbaikalia: (A) insect impression; (B) stereomicroscope view of the fore-gut with pollen grains; (C) pollen grains amassed at the hind end of the abdomen, (D) same, enlarged. Scale bars: 2 mm (A), 1 mm (B, C), 30 µm (D).

were taken at several places along the intestines to account for possible variations in the pollen load. For example, in the recently studied pollen load of *Ceroxyela dolichocera* Rasnitsyn, pollen grains are dispersed all over the intestines with the larger concentrations in the fore-gut and near the anus (Fig. 1). The pollen might have been taken at consecutive visits to the forage plant, yet no differences between the clumps have been revealed by microsampling. Pollen clumps and individual grains were mounted for light microscopy and scanning electron microscopy, as well as cut for transmission electron microscopy. Some pollen grains passed through the intestinal tract undamaged, while in other cases the external exinal layers were variously affected by digestion.

RESULTS

Pollen grains with banded (taeniate) surface structure form the most distinctive morphological group through the Permian extending to the Early Triassic. Taeniate morphologies are recorded from all parts of Laurasia as well as Gondwana, making the regional palynofloras more uniform than their contemporaneous macrofossil assemblages. Variation within the group involves configuration, density and regularity of the band patterns, providing generic distinctions (Figs 2A–D). The most common *Protohaploxypinus*-type grains with numerous uniform taeniae were produced by pteridosperms and glossopterids (Zavada 1991). *Lunatisporites*, with about four broad taeniae on the apertural face, is ascribed to the ullmannioid conifers (Balme 1995); at least some variants of a diverse *Vittatina* group with dense narrow bands associate with phylladoderms (Meyen 1987).

In the Kungurian of Tchekarda we found taeniate pollen grains in the gut compressions of *Idelopsocus* (Hypoperlida), *Parapsocidium* (Psocida), *Sojanidelia* (Grylloblattida), and *Sellardsiopsis* (Palaeomanteida, = Miomoptera). Among them, *Sellardsiopsis conspicua* was monophagous, with the pollen load consisting of *Protohaploxypinus* alone, while *Idelopsocus diradiatus* Rasnitsyn fed on both *Lunatisporites* and *Protohaploxypinus* (Rasnitsyn & Krassilov 1996*a*). *Sojanidelia floralis* Rasnitsyn was also oligophagous, with *Vittatina*-type and *Protohaploxypinus*-type taeniate grains mixed in the pollen load (Rasnitsyn & Krassilov 1996*b*). *Parapsocidium uralicum* G. Zalessky seemed to have been the only polyphagous insect, but taeniate grains constituted the major part of its diet, with a smaller contribution of discoid zonosaccate *Florinites–Cordaitina* type (Krassilov *et al.* 1999).

New groups of gymnosperms that appeared over the Permian–Triassic transition—the ginkgophytes, cycads, bennettites and czekanowskias—have produced rather uniform smooth anasulcate pollen, the ordinal affinities of which are scarcely recognizable in dispersed pollen assemblages. Despite their ubiquitous presence in the Mesozoic pollen samples and despite the fact that modern cycads are partly entomophilous, such pollen grains were never found in the guts of pollinivorous insects. The bennettitalean flower-like strobili might have been visited for nectar, but scarcely for pollen. In contrast, few Mesozoic morphotypes with distinctive surface features, such as *Classopollis* and *Eucommiidites*, were targeted by pollinivorous insects. Both rank among the most thoroughly studied charismatic types of extinct pollen morphotypes.

Plants producing *Classopollis*-type pollen are usually assigned to conifers (the Cheirolepidiaceae), although the pollen morphology is atypical for the group and is

TABLE 1. Insect fossils with the intestine pollen load preserved.

Insect taxon	n	Insect order	Locality	Age	Pollen taxon(s)	References
Permian						
Idelopsocus diradiatus Rasnitsyn	1	Hypoperlida	Tchekarda	Kungurian	*Lunatisporites*-type taeniate pollen: *Lunatisporites* sp., *Protohaploxypinus* sp., *Praecolpatites* sp. (rare)	Rasnitsyn & Krassilov 1996*a*
Parapsocidium uralicum G. Zalessky	1	Psocida	Tchekarda	Kungurian	*Protohaploxypinus*-type taeniate pollen: *Lunatisporites* sp. (dominant), *Protohaploxypinus perfecta* (Naumova) Samoilovich (subordinate), *Florinites luberae* Samoilovich (single grain), *Potoniesporites* sp. (single grain)	Krassilov *et al.* 1999
Sellardsiopsis conspicua G. Zalessky	1	Palaeomanteida	Tchekarda	Kungurian	*Protohaploxypinus*-type taeniate pollen: *Protohaploxypinus perfecta* (Naumova) Samoilovich	This paper
Sojanidellia floralis Rasnitsyn	1	Grylloblattida	Tchekarda	Kungurian	*Lunatisporites*-type taeniate pollen: *Lunatisporites* sp. (dominant), *Vittatina* cf. *fasciolata* (Balme et Hennedy) Bharadwaj (subordinate)	Rasnitsyn & Krassilov 1996*b*
Tillyardembia antennaeplana G. Zalessky	1	Grylloblattida	Tshekarda	Kungurian	*Cladaitina* sp.	Afonin 2000
Tshekardaenigma pollinivorum Rasnitsyn	1	Insecta *incertae sedis*	Tshekarda	Kungurian	Poorly preserved taeniate pollen	Rasnitsyn & Krassilov 1996*a*

TABLE 1. Insect fossils with the intestine pollen load preserved. (Continued)

Insect taxon	n	Insect order	Locality	Age	Pollen taxon(s)	References
Jurassic						
Aboilus amplus Gorochov	1	Orthoptera	Karatau	Late Jurassic	*Classopollis*-type rimulate pollen: *Classopollis* sp.	Krassilov *et al.*, 1997
Aboilus sp. aff. *dilutus* Gorochov	1	Orthoptera	Karatau	Late Jurassic	*Classopollis*-type rimulate pollen: *Classopollis* sp.	Krassilov *et al.* 1997
Phasmomimoides minutus Gorochov	1	Phasmatida	Karatau	Late Jurassic	leaves of ?*Pagiophyllum* cf. *peregrinum* Lindl. et Hutt. with adhered pollen grains of *Classopollis* type	Krassilov & Rasnitsyn 2000
Brachyphyllophagus phasma Rasnitsyn	1	cf. Embiida	Karatau	Late Jurassic	leaves of ?*Brachyphyllum* with adhered pollen grains of *Classopollis* type	Krassilov & Rasnitsyn 2000
Brachyphyllophagus phantasus Rasnitsyn	1	cf. Embiida	Karatau	Late Jurassic	leaves of ?*Brachyphyllum* leaves with adhered pollen grains of *Classopollis* type	Krassilov & Rasnitsyn 2000
Cretaceous						
Ceroxyela dolichocera Rasnitsyn	1	Hymenoptera	Baissa	Early Cretaceous	*Eucommiidites*-group pollen: *Cryptosaccites pabularis* Krassilov et Tekleva	Krassilov *et al.* 2003
Ceroxyela dolichocera Rasnitsyn	1	Hymenoptera	Baissa	Early Cretaceous	*Vitimipollis edulis* Krassilov	Krassilov & Rasnitsyn 1982
Anthoxyela anthophaga Rasnitsyn	1	Hymenoptera	Baissa	Early Cretaceous	*Alisporites alimentosus* Krassilov	Krassilov & Rasnitsyn, 1982
Spathoxyela pinicola Rasnitsyn	1	Hymenoptera	Baissa	Early Cretaceous	*Pinuspollenites entomophilus* Krassilov	Krassilov & Rasnitsyn 1982

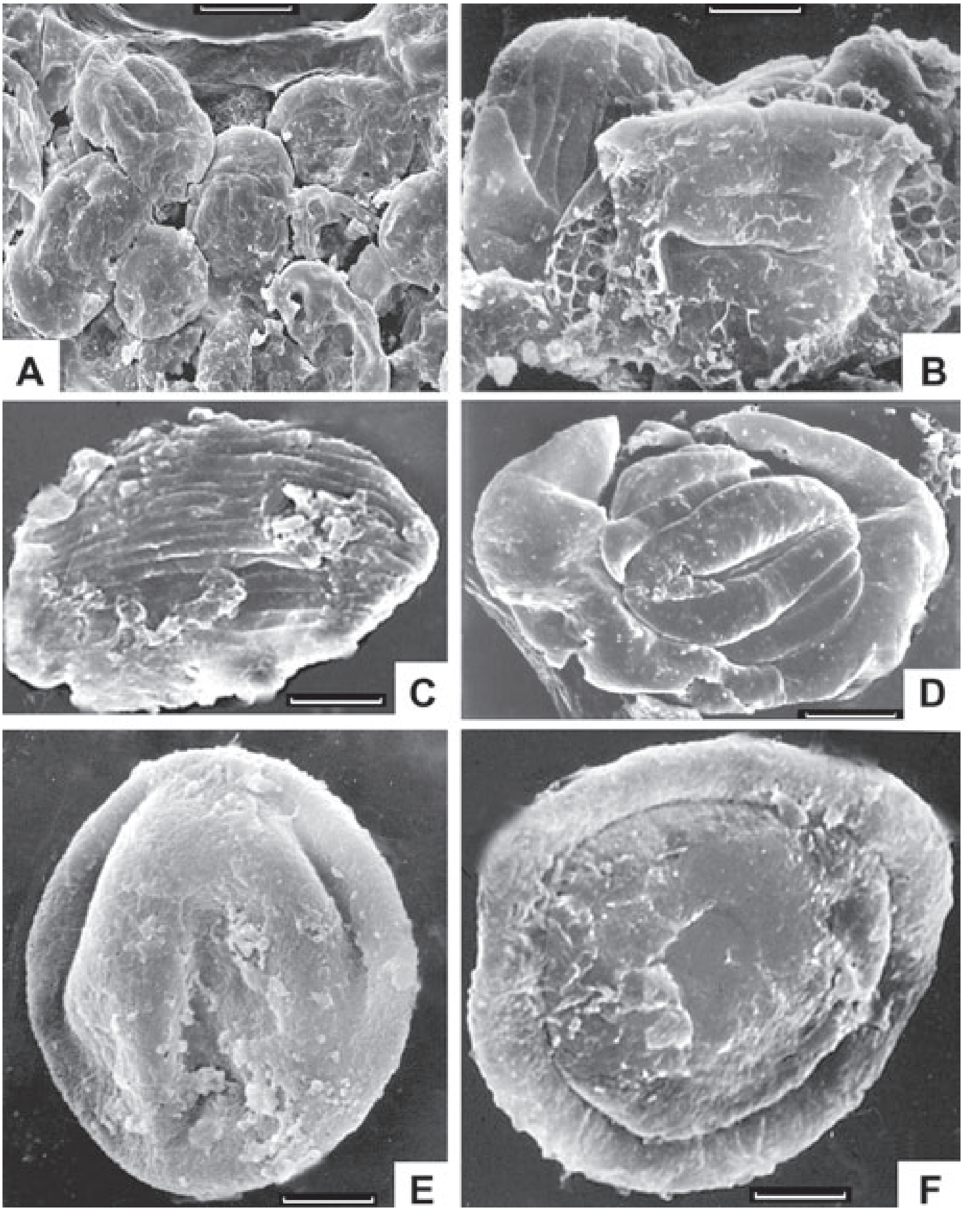

Fig. 2. Pollen loads of Palaeozoic and Mesozoic insects: (A) *Protohaploxypinus*-type taeniate pollen from *Sellardsiopsis conspicua* G. Zalessky, Lower Permian Tchekarda locality; (B) *Protohaploxypinus*-type taeniate pollen from *Parapsocidium uralicum* G. Zalessky (Psocida), same locality; (C) *Vittatina*-type taeniate pollen from *Sojanidelia floralis* Rasnitsyn (Grylloblattida), same locality; (D) *Lunatisporites*-type taeniate pollen from *Idelopsocus diradiatus* Rasnitsyn, same locality; (E) *Eucommiidites*-group pollen (*Cryptosaccites pabularis* Krassilov et Tekleva) from *Ceroxyela dolichocera* Rasnitsyn (Xyelidae, Hymenoptera), Lower Cretaceous Baissa locality, Transbaikalia; (F) *Classopollis*-type rimulate pollen from *Aboilus* cf. *dilutus* Gorochov (Orthoptera, katydids), Upper Jurassic of Karatau, Kazakhstan. Scale bars: 30 µm (A), 10 µm (B–F).

more consistent with a gnetalean affinity, suggested by Krassilov (1982) on account of ovuliferous organs. Morphologically, *Classopollis* belongs to a group of rimulate pollen with a distinctive subequatorial furrow dividing the globular grain into somewhat unequal hemispheres. The furrow is aligned with a striate equatorial ring, or cingulum, probably derived from the annular saccus of *Florinites*-like Palaeozoic predecessors. The distal hemisphere is marked by a circular pore; the proximal one, with a triangular scar revealing filaments that bound the tetraspores of a persistent tetrad.

It has been repeatedly suggested that *Classopollis*-producing plants might have been entomophilous, and our find of this type of pollen in the guts of Jurassic insects has provided additional evidence (Krassilov *et al*. 1997). In the Late Jurassic of Karatau, representatives of the grasshopper-like genus *Aboilus* (Orthoptera, katydids) were the most vigorous *Classopollis* eaters (Fig. 2F), while *Brachyphyllophagus* (Gryllones, possibly related to Embiida, the webspinners), might have consumed such pollen together with *Brachyphyllum*-type scale-leaves of the same plant (Krassilov & Rasnitsyn 2000).

Eucommiidites, with three furrows, was initially described as angiospermous, but was then found in the pollen chambers of some Jurassic and Cretaceous ovules. Therefore it appears to belong to a plant group with gymnospermous fertilization (Hughes 1961), most probably of gnetalean affinities. Yet, as was probably the case with the other charismatic pollen types, *Eucommiidites* morphology might have appeared by parallel development in different lineages of Mesozoic gymnosperms.

We studied *Eucommiidites*-type grains (though much larger than in the type species *E. troedssonii*) from gut compressions of a xyelid species, *Ceroxyela dolichocera* (Fig. 2E) from the Lower Cretaceous of Baissa locality, Transbaikalia (Krassilov *et al*. 2003). Ultrastructural studies revealed a vestigial saccus, while the lateral furrows were leptomatic, containing residual sexinal elements. *Ceroxyela dolichocera* also fed on the less distinctive saccate pollen grains produced by proangiospermous plants with monoclinous (bisexual) flowers.

DISCUSSION

We have found that Palaeozoic and Mesozoic pollinivorous insects preferred ornamented pollen grains. Some of them foraged for pollen grains with a specific surface pattern. It is well known that pollen spread by insects usually has surface structures increasing its stickiness (Faegri & Van Der Pijl 1966). However, in the case of taeniate pollen grains, *Classopollis* (with the rare exception of spinulate grains) and *Eucommiidites*, surface patterns had nothing to do with stickiness. Rather they were for visual and/or tactile perception. Although it has been repeatedly suggested that ornamented exines might have been related to arid climate, they have also been recorded from coal-bearing deposits. Moreover, the utility of taeniae, rimulae, cinguli, etc. as volume-regulated features has never been confirmed by any present-day examples.

In the Permian and early Mesozoic gymnosperms, the pollen-bearing structures were cones of peltate sporangiophores. In the absence of pollen, even an experienced morphologist would have difficulties in determining them. These organs were not distinctive enough to serve as pollen guides. At close quarters, this function was compensated by specific pollen ornamentation that might have developed and differentiated primarily for this purpose.

Several problems arising in respect to the Permian taeniate pollen morphologies—their parallel development in several gymnosperm lineages, their spread over the major phytogeographical boundaries, and their differentiation into a number of morphotypes, differing mainly in the band configuration—might have been related to pollinivory.

We hypothesise that prior to the advent of angiosperms, a mechanism of plant–insect co-evolution was at work, requiring recognition of pollen surface patterns on the part of pollinivorous insects and diversification of such patterns on the part of their forage plants. For the latter, acquisition of a recognisable surface pattern conferred the advantage of acquiring a specific pollen vector. Vicariant plant groups might have benefited in having similar pollen surface patterns when pollinated by one and the same group of insects. With the rise of angiosperms, this mechanism was replaced by recognition of flower/inflorescence patterns at a greater distance and was eventually lost.

CONCLUDING REMARKS

Spread of pollen morphologies with easily recognisable surface patterns, most conspicuously the Permian taeniate pollen grains, but also the Mesozoic *Eucommiidites* and possibly *Classopollis*, across gymnosperm lineages, is hitherto an ill-understood evolutionary phenomenon. An attempt to explain the appearance of sculptured Palaeozoic and Mesozoic pollen grains as an adaptation to arid climate failed on account of the diversity of their geographic and facial occurrences, ranging from temperate to tropical zones and from salt-bearing to coal-bearing deposits. Insofar as such pollen grains have been found in pollen loads of fossil insects, plant–insect co-evolution might have been involved in their origins. We hypothesise that, in the absence of floral cues, a visual or tactile recognition of preferable pollen (also, as one of the referees suggested, an egress of olfactory cues from taeniate pollen) played a leading role in plant–insect interaction, encouraging the development of certain types of surface structures. There must be alternative explanations, but a mere coincidence of pollen morphology and the dietary preferences in insects or a direct adaptation to climatic conditions are unlikely as candidates for such.

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